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An experimental study of spiders in a shrub-steppe ecosystem: the effects of prey availability and shrub architecture

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Abstract. Habitat structure is of great importance for the distribution and abundance of various organisms. Spiders are especially sensitive to structural features of their environment. Although spiders are influenced by habitat structure, it remains unclear whether spiders respond to architecture, to differences in prey availability associated with different architectures, or both. Here, we investigated the effects of shrub architecture and prey availability and their interactions on a spider community in a shrub-steppe environment in northern Utah, USA. Big sagebrush shrubs, matched by size, were randomly assigned to six experimental treatments: two levels of prey attractant (shrubs were either baited or not baited) and three levels of foliage density (low, natural/control, or high). We found that spider abundance and species richness were affected by both prey availability and shrub architecture, while variation in spider species diversity (Shannon-Wiener index) was governed by changes in shrub architecture. Spider species and family compositions were also associated with changes in shrub architecture, although guild composition was not. We discuss the implications and limitations of these findings and present suggestions for future research.

Keywords: Habitat structure, spider prey, Araneae, sagebrush

Ecologists have long been interested in patterns of community structure and the mechanisms that generate these patterns (Hutchinson 1959). Community structure is the result of interactions among many factors, making it difficult to assess the relative contribution and importance of any one factor (Uetz 1991). Clearly, if we are to understand and manage communities, there is a need to disentangle the different ecological factors that shape their composition.

Habitat structure, defined as the physical composition and arrangement of objects in space and time, is one of several factors considered important in influencing the distribution and abundance of animals (McCoy & Bell 1991). Structurally complex habitats provide animals with a wider array of microhabitats, more diverse ways of exploiting food resources, amelioration of climatic extremes, and protection from predators (see reviews in Bell et al. 1991). Habitat structure influences a variety of organisms, including birds (MaeArthur & MacArthur 1961), lizards (Pianka 1966) and various invertebrates (Lawton 1983), including spiders (Uetz 1991; Wise 1993).

Spiders are influenced by several structural attributes of the environment, including vegetation density and height (Hatley & MacMahon 1980; Abraham 1983; Brierton et al. 2003), as well as interactions among variables such as branch height and orientation (Heikkinen & MacMahon 2004). Spiders may even distinguish between different branch types, with some spiders being more common on reproductive than on vegetative branches (de Souza & Martins 2004).

Although spider communities differ with changes in habitat architecture, it remains unclear whether spiders are responding to architecture per se or to differences in prey availability caused by different architectures. Although some studies suggest that prey availability is important in understanding patterns of spider community structure (Riechert 1974; Horváth et al. 2005), others emphasize that prey availability is of lesser importance and that spider communities are shaped primarily by habitat structure (Greenstone 1984; Halaj et al. 2000; Chan et al. 2009). These findings highlight the need to further evaluate the processes responsible for structuring spider communities.

Our goal for this study was to investigate the relative importance of prey availability and shrub architecture in determining the composition of a well-studied spider community in a shrub-steppe environment in northern Utah, USA. Spiders are model organisms for addressing ecological studies. They are ubiquitous, locally abundant, taxonomically diverse, and amenable to experimental manipulations (Hatley & MacMahon 1980; Wise 1993). Spiders are especially well-suited for investigating the effect of shrub architecture on community organization because, as carnivores, they are not directly reliant on a particular plant species as a food source (Hatley & MacMahon 1980) and, for web-builders, the building of a web often requires specific substrates for attachment (Uetz 1991).

METHODS

Study site.—Our research expands upon earlier studies of spider communities in the Great Basin shrub-steppe ecosystem of northern Utah (Hatley & MacMahon 1980; Robinson 1981; Abraham 1983; Wing 1984; Ehmann & MacMahon 1996; Heikkinen & MacMahon 2004). This study was conducted at Hardware Ranch Wildlife Management Area (41.61° N, 111.57° W). Hardware Ranch WMA is located in the Wasatch-Cache National Forest, about 40 km southeast of Logan, Cache County, Utah and is managed by the Utah Division of Wildlife Resources. The site is at an elevation of 1731 m and is dominated by big sagebrush (*Artemisia tridentata*) and low sage (*Artemisia arbuscula*). The land is used primarily as winter range for big game.

Shrub selection.—To reduce the heterogeneity among individual shrubs, we applied several criteria when selecting shrubs. Experimental shrubs (*A. tridentata*) had a single trunk at ground level, were not in immediate contact with an adjacent shrub and were at least 10 m from another

experimental shrub. We measured shrubs before and after treatment for maximum canopy width, width perpendicular to maximum canopy width and canopy height (excluding the trunk beneath) (Hatley & MacMahon 1980). Only shrubs with all three canopy dimensions between 0.4 and 1 m were selected. Shrub volume was determined by using the formula for an ellipsoid

$$volume = 4/3\ \pi\ a\ b\ h$$

where a and b represent, respectively, the linear dimensions of the major and minor axes, and h represents height.

Study design and treatments.—We permanently identified shrubs selected for study with a numbered tag to facilitate location and data collection and then randomly assigned them to six experimental treatments, with 25 replieates per treatment. Experimental treatments consisted of factorial combinations of two levels of prey attractant and three levels of foliage density. Prey attractant treatments included shrubs that were either baited or not baited. The purpose of the bait was to inerease the probability of prey visits and/or the duration of each visit (Wing 1984). Baited shrubs contained four suspended containers: two (59 ml) containers filled with pig offal, one (22 ml) container filled with yellow banana-oil flavored honey, and one (22 ml) container filled with red-colored honey. Container lids were perforated to facilitate odor dispersion. As a control, identical but empty containers were suspended from shrubs not baited. We baited shrubs two weeks prior to sampling to maximize arthropod abundance on shrubs (Robinson 1981).

Shrub architecture was manipulated to either increase or decrease shrub foliage density (Hatley & MacMahon 1980). We increased foliage density by tightly binding all branches together (hereafter referred to as "high") and decreased density by clipping shrub foliage ("low"). Shrubs not manipulated were used as controls ("natural"). Shrubs were manipulated in spring of 2007 and 2008. We calculated differences in shrub foliage density using photographs taken from a digital camera (Nikon Coolpix L12) positioned approximately 1.5 m from the shrub. A white cloth attached to a wooden frame (1.5 × 1.5 m) was positioned behind the shrub and before and after treatment pictures were taken. Pictures were taken again at the end of the first sampling season. The pictures were imported into Adobe Photoshop CS4. Here, shadows surrounding the shrub were first removed using the 'color range' option. Images were then transformed into a black and white image by means of the 'threshold' option and the area occupied by the shrub was outlined using the magnetic 'lasso' tool. The 'histogram' tool was then used to determine the ratio of white (background) vs. black (vegetation) pixels. For each picture, this procedure was carried out twice and the average was taken.

Determination of sampling effort.—Before experimental manipulations, we sampled fifty randomly chosen shrubs to obtain a preliminary survey of the spider community. A species accumulation curve was then generated. Species accumulation curves show the rate at which new species are found by plotting the cumulative number of observed species as a function of sampling effort (Magurran 2004). As sampling efforts increase and as fewer new species are found, the curve approaches an asymptote, indicating that a representative sample was achieved given the collection method used. Here, we determined that a sampling effort of 25 shrubs per treatment combination was sufficient. Species accumulation curves were generated using the 'specaccum' function in the 'vegan' package (Oksanen et al. 2010) of R environment (R Development Core Team 2011).

Sampling of arthropods.—We sampled shrubs during a five-day sampling period once a month in June, July, August and September of 2007 and 2008. September samples from both years and a few samples from the remaining collections were discarded because of bait disturbances. Sampling periods took place at intervals of no less than three weeks. Sampling began approximately two hours after sunrise, occurred only when there was an absence of high winds and precipitation, and did not occur when temperatures were below 10 °C. We collected arthropods by using the beating technique (Ehmann & MacMahon 1996). Each shrub was quickly surrounded at the base with a canvas sheet (1.5 × 1.5 m) and then beaten 15 times with an ax handle to dislodge specimens onto the beating sheet for collection. Specimens were collected with an aspirator and immediately preserved in vials containing 70% ethanol. After the arthropods from the first beating were collected, a second beating episode of the same duration followed. The double-beating method was used previously and resulted in a 100% collection rate (Ehmann & MacMahon 1996).

Since this sampling technique may emphasize sedentary prey while ignoring highly active prey, sticky traps were also used to monitor prey availability. A sheet of clear plexiglass (25 × 25 cm) was coated on both sides with Tanglefoot® trap coating (Tanglefoot Co., Grand Rapids, MI) and attached to two vertical stakes (Greenstone 1984; Halaj et al. 2000). During July of 2007, we placed one trap next to each of five randomly chosen shrubs from each treatment type not sampled by the beating technique. Each trap was positioned 20 cm from a given shrub, and the cardinal direction of the trap was determined at random. After five days, the traps were collected and taken to the laboratory (Wing 1984). These traps may not mirror suitable prey or the exact resource base available to spiders, but they do allow for the analysis of specimens active at a given time and place (Rypstra 1986).

We identified spiders to species and measured their body length (not including spinnerets) to the nearest 0.1 millimeter. We excluded immature spiders from analyses, since their behavior and habitat may differ from adults, but also because some immature spiders were difficult to identify to species (Sacket et al. 2008).

We further sorted spiders into a priori guilds, or groups of organisms that exploit the same resource in similar ways (Root 1967). These assignments are user-defined parameters widely used in community studies (Hawkins & MacMahon 1989). For spiders, guild membership is based on observations of foraging techniques that are often reinforced by morphological characteristics shared at the family level (Post & Riechert 1977). However, since there are no absolute guidelines, spider guild assignments vary widely (Uetz et al. 1999). In this study, two different approaches for the classification of spider foraging guilds were used. Following the classification proposed by Uetz et al. (1999), we grouped spider families into the following four guilds: 1) ambushers: Philodromidae and Thomisidae; 2) runners: Gnaphosidae and Lycosidae; 3)

stalkers: Mimetidae, Oxyopidae and Salticidae; and 4) trappers: Araneidae, Dictynidae, Linyphiidae and Theridiidae. The second approach followed the classification commonly used for spiders on big sagebrush (Hatley & MacMahon 1980; Robinson 1981; Wing 1984; Heikkinen & MacMahon 2004), where members from the family Philodromidae were analyzed as runners instead of ambushers. Relationships between spider hunting strategies and spatial characteristics of the vegetation have previously been described. In general, ambushers prefer dense foliage, stalkers and trappers prefer open foliage, and runners prefer a variety of foliage types (Hatley & MacMahon 1980; Uetz et al. 1999).

We identified potential prey items to the order level or below and assigned them to the following functional groups: detritivores, herbivores (including pollinators) and natural enemies (predators and parasites/parasitoids). Prey composition was examined to assess whether differences among treatments, if present, correspond to variations in spider community structure. Taxonomic classification followed Triplehorn & Johnson (2005), and functional group assignments were based on dietary information provided also by Triplehorn & Johnson (2005). We did not collect ants (Hymenoptera: Formicidae) or aphids (Hemiptera: Aphididae) because their high abundanees made collection of samples in a short period of time difficult. All specimens were deposited in the Department of Biology at Utah State University for reference.

Data analyses.—We compared mean shrub foliage density among treatments with a repeated measures one-way analysis of variance (ANOVA). Relevant pairwise comparisons were made as needed and family-wise Type I errors were controlled by applying the Tukey-Kramer method. An unstructured covariance matrix was selected to model repeated measures across the three measurements based on Akaike's Information Corrected Criterion (AIC_C). A two-way ANOVA, with foliage density and prey attractant treatments as factors, was used to analyze square-root transformed sticky trap data. The ANOVAs were performed using the MIXED procedure in SAS/STAT software Version 9.2 in the SAS System for Windows (SAS Institute 2011).

We tested the effects of foliage density and prey attractant treatments on spider and potential prey abundance, as well as spider species diversity and richness, using a general linear mixed model (LMM) with repeated measures. Spider diversity was determined using the Shannon-Wiener diversity index (Magurran 2004), and spider and potential prey abundances were converted into densities (individuals per m^3) to account for differences in shrub volume. Experimental treatments were treated as fixed factors, while shrubs were incorporated in the model as a random effect and treated as independent replications. An unstructured covariance matrix was used to model repeated measures across three months in each of two years. Response variables were ln-transformed ($x + 1$) to improve model performance. For main effects, pairwise mean comparisons were adjusted for family-wise Type I errors using the Tukey-Kramer method. Pairwise comparisons for significant interaction terms were examined with stepdown Bonferroni adjustments. Analyses were carried out using the MIXED procedure in SAS/STAT software (SAS Institute 2011).

Experimental foliage treatments did not produce shrubs of equal density within each treatment group. Likewise, prey density varied among shrubs within a treatment group. Hence, because continuous variables may be more informative than discrete levels, we also analyzed data using regression analyses. Spider density, diversity, and richness were regressed on continuous measures of foliage density and prey density using multiple linear regression, and prey density was regressed on foliage density using simple linear regression. Since foliage densities were not measured consecutively across sampling periods, spider and prey densities were averaged for shrubs sampled during all sampling periods. Natural-log transformations were applied to averaged spider and prey densities to satisfy statistical assumptions. Regression analyses were performed using the REG procedure in SAS/STAT software (SAS Institute 2011).

To test the hypothesis that spider and potential prey community composition differed among experimental treatments, we used a permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001). PERMANOVA differs from traditional multivariate analysis of variance (MANOVA) by relaxing the assumptions of a multivariate normal distribution. Computations were performed using the 'adonis' function in the 'vegan' package of R environment (R Development Core Team 2011), and significance values were generated using 1000 permutations (Oksanen et al. 2010). We then used a similarity of percentages (SIMPER) analysis to determine which taxa contributed to overall differences in community composition. Taxa contributing $\geq$ 5% to the between group dissimilarities were highlighted. SIMPER tests were carried out using the program PRIMER v. 6 (Clarke & Gorley 2006).

We illustrated differences in compositional patterns with non-metric multidimensional scaling (NMDS) plots using the 'metaMDS' function in the 'vegan' package of R (R Development Core Team 2011) (Oksanen et al. 2010). NMDS arranges objects (i.e., sites) in multidimensional space so that points in close proximity are more similar (e.g., in species composition) than those further apart. NMDS is considered to be one of the most robust ordination techniques available because it is well suited for non-normal data and does not assume linearity between species and environmental gradients (McCune & Graee 2002).

Multivariate analyses were performed using pooled densities for shrubs sampled during all sampling periods. Prior to analyses, data were square-root transformed to reduce the influence of the most abundant taxa, then standardized by sample (i.e., shrub) to minimize differences in total abundance (McCune & Grace 2002). Distance matrices were calculated using the Bray-Curtis dissimilarity index, and taxa represented by less than 10 individuals were removed from the data set (McCune & Grace 2002).

Significant differences in results refer to a statistical significance of $P \leq 0.05$. Unless otherwise specified, data are presented as mean $\pm$ standard error.

RESULTS

Shrub manipulations.—Architectural treatments were designed to modify foliage densities. Shrub foliage densities were similar among treatment groups prior to experimental manipulations (ANOVA, $F_{2,147} = 0.5$, $P = 0.58$). Following manipulations, low and high foliage density shrubs were

different from their initial foliage densities; and foliage densities for each architectural treatment were different from the other two treatments, with differences persisting at the end of the sampling season (all $P < 0.001$). Low foliage density shrubs averaged a 13.5% loss of density (i.e., vegetation pixels), while high foliage density shrubs showed an 8.4% gain in density.

Potential prey density and community composition.—A total of 9929 potential prey were collected, representing 15 orders and more than 66 families (see Appendix 1). Leafhoppers (Hemiptera: Cicadellidae), plant bugs (Hemiptera: Miridae) and leaf beetles (Coleoptera: Chrysomelidae) comprised over 77% of the non-Araneae arthropods collected.

Potential prey densities were influenced by the interaction between foliage density and prey attractant (LMM, $F_{2,125} = 3.5$, $P = 0.035$). With the exception of natural foliage density shrubs, baiting shrubs did not suceeed in changing the prey base. Low and high foliage density shrubs contained fewer prey items with the introduction of prey attractant, while natural foliage density shrubs contained more prey when shrubs were baited than when they were not (Fig. 1A). In addition, the main effect of prey attractant was not statistieally significant (LMM, $F_{1,125} = 0.02$, $P = 0.90$), although the main effect of foliage density was highly significant (LMM, $F_{2,125} = 17.6$, $P < 0.001$). More prey items were collected in high foliage density shrubs than in natural or low foliage density shrubs, and natural foliage density shrubs contained more prey than low foliage density shrubs. Prey densities were also influenced by the interaction between year and month of data collection (LMM, $F_{2,127} = 60.6$, $P < 0.001$). Prey densities declined from June to August of 2007, but were similar across months in 2008 (Fig. 1B). A simple regression analysis also revealed an influence of foliage density on prey density (regression equation: $\ln(y) = 1.333 + 0.034$ (foliage density), $R^2 = 0.12$, $P < 0.001$). Lastly, sticky traps did not detect significant differenees in potential prey densities among foliage density and prey attractant treatments (ANOVA, main effects and interaction, $P > 0.1$). Only one spider was collected from the sticky traps.

Potential prey community composition did not differ among foliage density and prey attractant treatments, either at the level of orders or by functional group (PERMANOVA, main effects and interaction, $P > 0.1$).

Spider density, diversity, and community composition.—A total of 6262 spiders were collected, of which 4518 (72%) individuals were immature. Of adult specimens, 31 speeies were collected (see Appendix 2). Members from the family Salticidae were numerically dominant (48%), followed by Philodromidae (21%), Dictynidae (9%), Oxyopidae (8%) and Theridiidae (6%). Families Araneidae, Gnaphosidae, Linyphiidae, Lycosidae, Mimetidae and Thomisidae were also collected, although in fewer numbers. The five most abundant species were *Pelegrina clemata* (Levi & Levi 1951) (Salticidae), *Philodromus histrio* (Latreille 1819) (Philodromidae), *Ebo pepinensis* Gertsch 1933 (Philodromidae), *Oxyopes scalaris* Hentz 1845 (Oxyopidae) and *Emblyna reticulata* (Gertsch & Ivie 1936) (Dictynidae); which together characterized 70% of the adult spiders collected.

Spider densities were influenced by foliage density treatment (LMM, $F_{2,139} = 22.1$, $P < 0.001$). More spiders were collected in high foliage density shrubs than in natural or low foliage density shrubs, and natural foliage density shrubs contained more spiders than low foliage density shrubs (Fig. 2A). A multiple regression analysis showed that spider density was associated with both foliage density and prey density ($P = 0.005$ and < 0.001, respectively) (regression equation: $\ln(y) = -1.557 + 0.023$ (foliage density) $+ 0.502 \cdot \ln$ (prey density), $R^2 = 0.34$), although the LMM main effect of prey attractant treatment on spider densities was not significant ($F_{1,139} = 1.0$, $P = 0.31$), nor was the interaction between the two factors ($F_{2,139} = 1.7$, $P = 0.19$). Spider density was also influenced by year and month of data collection (LMM, $F_{2,138} = 4.1$, $P = 0.018$). Spider densities declined from June to August of 2007, but were static across months in 2008 (Fig. 2B).

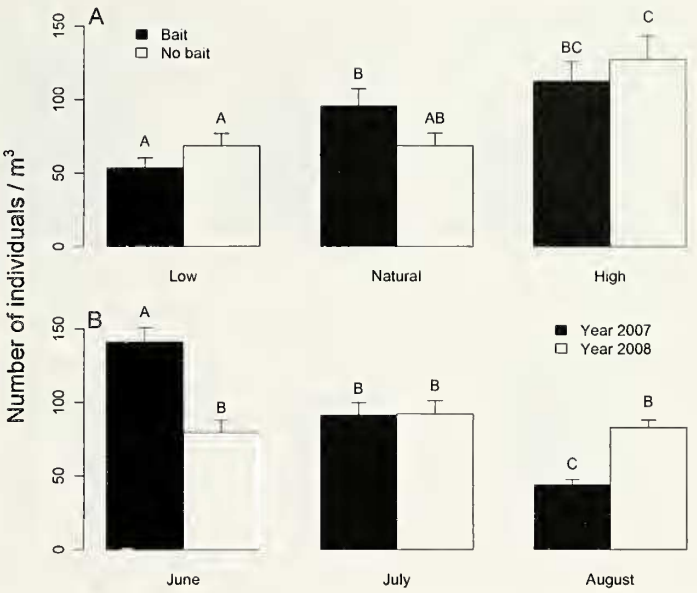

Figure 1.—Potential spider prey densities sorted by A) different foliage density and prey attractant treatments and B) year and month of collection. Graphs show means with standard errors. Different letters indicate a significant differenee at $P < 0.05$. Means and standard errors were back-transformed from ln-transformed estimates.

Spider species diversity (H′) differed by month of collection (LMM, $F_{2,114} = 8.0$, $P < 0.001$) and by foliage density treatment (LMM, $F_{2,108} = 3.1$, $P = 0.048$). Spiders reached their highest diversity in June (mean Shannon index ± SE: 0.90 ± 0.03), followed by July (0.77 ± 0.03) and August (0.77 ± 0.03). Spiders were also more diverse on high and natural foliage density shrubs (0.86 ± 0.01 and 0.82 ± 0.07, respectively) than on low foliage density shrubs (0.75 ± 0.02). A multiple regression analysis showed that spider diversity was associated with foliage density ($P < 0.001$), but not with prey density ($P = 0.24$) (regression equation: $y = -0.471 + 0.01$(foliage density), $R^2 = 0.13$).

Spider species richness was influenced by year and month of collection (LMM, $F_{2,140} = 4.9$, $P = 0.009$), as well as foliage density treatment ($F_{2,139} = 15.4$, $P < 0.001$). More species were collected during June (mean number of species ± SE: 6.62 ± 0.09) than July (6.20 ± 0.07) and August (6.14 ± 0.06), with species richness being higher in June 2007 (6.90 ± 0.12) than in June 2008 (6.35 ± 0.11). More species were also collected on natural and high foliage density shrubs (6.63 ± 0.10 and 6.42 ± 0.10, respectively) than on low foliage density shrubs (5.93 ± 0.09). A multiple regression analysis revealed

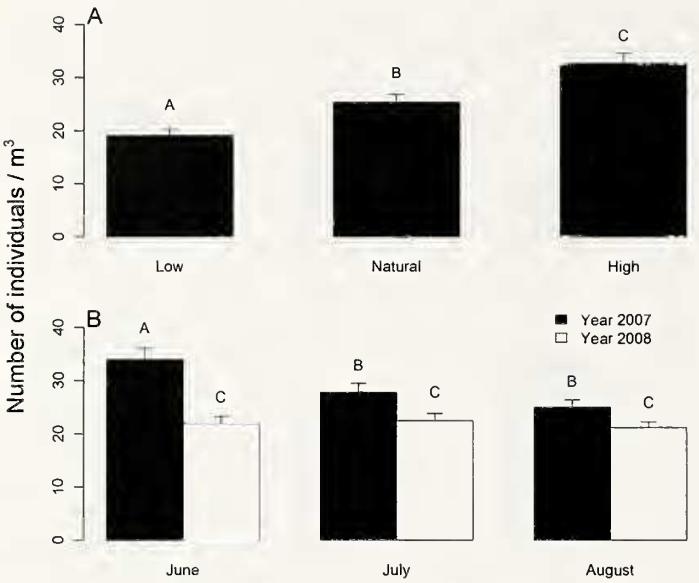

Figure 2.—Spider densities sorted by A) different foliage density treatments and B) year and month of collection. Graphs show means with standard errors. Different letters indicate a significant difference at $P < 0.05$. Means and standard errors were back-transformed from ln-transformed estimates.

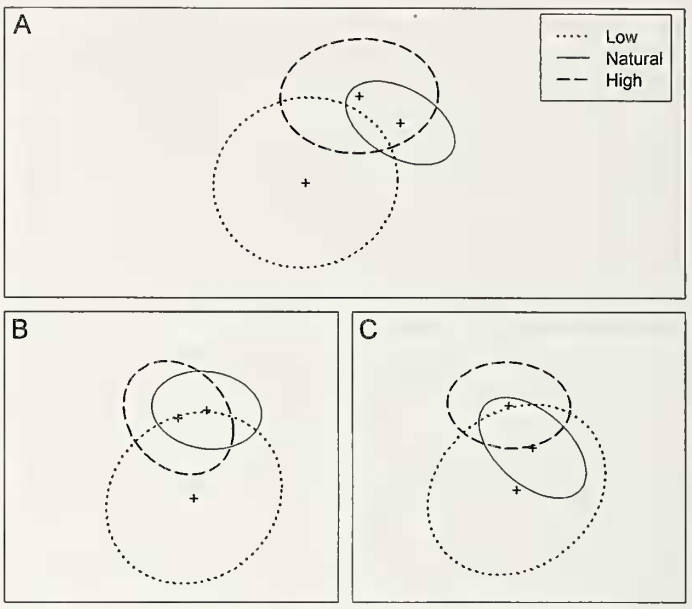

Figure 3.—Non-metric multidimensional scaling (NMDS) plots representing variation in A) spider species composition, B) spider family composition, and C) spider guild composition, where guild composition followed the classification proposed by Uetz et al. (1999). Foliage density is plotted as centroids (+ symbols) and 95% confidence ellipses of the mean sample score. Confidence ellipses are for visualization only; actual significance tests were obtained from PERMANOVA analyses (see Table 1 for R^2 and significance values). Final stress for a two-dimensional (2D) solution was 21.66 for the species ordination, 21.48 for the family ordination, and 11.25 for the guild ordination.

that spider species richness was related to both foliage density and prey density ($P = 0.012$ and 0.001, respectively) (regression equation: $y = -1.244 + 0.02$ (foliage density) + 0.262•ln (prey density), $R^2 = 0.17$).

Spider species composition varied with foliage density (Table 1, Fig. 3A). A SIMPER analysis indicated that natural and high foliage density shrubs were more similar to each other in species composition than either treatment was to low foliage density shrubs (Table 2). Low foliage density shrubs differed from natural and high foliage density shrubs by having higher relative abundances of *P. clemata* (Salticidae) and *Metepeira foxi* Gertsch & Ivie 1936 (Araneidae) and lower relative abundances of *Ph. histrio* (Philodromidae), *E. pepinensis* (Philodromidae), *O. scalaris* (Oxyopidae) and *Dipoena nigra* (Emerton 1882) (Theridiidae).

Family composition also varied with foliage density (Table 1, Fig. 3B). A SIMPER analysis showed that natural and high foliage density shrubs were more similar to each other in family composition than either treatment was to low foliage density shrubs (Table 3). Low foliage density shrubs differed from natural and high foliage density shrubs by having higher relative abundances of jumping spiders (Salticidae) and orb-weavers (Araneidae) and lower relative abundances of Oxyopidae, Philodromidae, and Theridiidae. Dictynids were more abundant on natural foliage density shrubs.

Experimental treatments had no effect on spider guild composition, regardless of classification used (Table 1, Fig. 3C). In general, the distribution of spider guilds was similar across treatments.

DISCUSSION

Habitat structure is cited as an important factor in the distribution and abundance of various organisms (see reviews in Bell et al. 1991). Results presented here demonstrate that spider density and species richness and diversity (H′) are influenced by changes in shrub architecture. High foliage density shrubs supported more spiders and more species than structurally less complex habitats (i.e., low and natural foliage density shrubs). Our results are generally consistent with other studies involving structural influences of vegetation on spiders (Hatley and MacMahon 1980; Greenstone 1984; Brierton et al. 2003). This pattern of greater abundance and diversity on more dense or structurally complex habitats often is attributed to the availability of more microhabitats or as a way to partition resources and reduce interspecific competition (Uetz 1991; Wise 1993).

Variations in spider species and family composition were also observed and were caused by changes in relative abundances, rather than differences in taxonomic composition. For example, although *P. clemata* (Salticidae) was the most frequently captured spider on all shrub types, its relative abundances were higher on low foliage density shrubs. Open substrates may collect a higher proportion of jumping spiders, since dense branching can obstruct their vision and impede their ability to capture prey (Hatley & MacMahon 1980). Since jumping spiders are active hunters that leap onto prey, more compact branching may further interfere with their ability to jump (Stratton et al. 1979). Structurally simple environments also supported relatively more orb-weaving spiders. Wide gaps between shrub branches are considered structurally more suitable for the building of large orb webs than shrubs with more dense architectures (Hatley & MacMahon 1980; Marc & Canard 1997) and may also be associated with larger species of web builders (Hatley & MacMahon 1980).

Table 1.—R^2 and P values from PERMANOVA analysis of spider species, family, and guild composition. For guild composition, values preceding a slash indicate results following the classification proposed by Uetz et al. (1999), whereas values following a slash indicate results when guild assignments followed the classification used for spiders on big sagebrush. PERMANOVA analyses are based on Bray-Curtis dissimilarities.

	Species		Family		Guild	
	R^2	P	R^2	P	R^2	P
Foliage density treatment (FDT)	0.043	0.004	0.045	0.003	0.023 / 0.028	0.245 / 0.176
Prey attractant treatment (PAT)	0.010	0.316	0.010	0.354	0.011 / 0.012	0.317 / 0.264
FDT × PAT	0.013	0.677	0.024	0.163	0.028 / 0.026	0.144 / 0.190

Structurally diverse environments, on the other hand, may be chosen by species that attack their prey within close proximity. For example, although thomisids were largely underrepresented in this study, they are thought to prefer more concealed locations for prey capture (Hatley & MacMahon 1980; Uetz 1991). Space-web builders (Dictynidae and Theridiidae) may also require more complex substrates, since they tend to build three-dimensional webs that occupy small spaces between branches (Stratton et al. 1979; Marc & Canard 1997).

Despite notable differences in spider species and family composition, guild composition did not vary by foliage type. These results contradict previous studies suggesting that habitat structure influences the distribution of spider guilds found on big sagebrush (Hatley & MacMahon 1980; Robinson 1981; Abraham 1983; Wing 1984; Heikkinen & MaeMahon 2004) and elsewhere (Uetz et al. 1999; Brierton et al. 2003). Discrepancies between research findings may have been due to underlying differences in field site characteristics. Previous studies in northern Utah were mostly conducted at sites with elevations more than 200 m below our study area (Hatley & MacMahon 1980; Robinson 1981; Abraham 1983; Wing 1984). Since spider composition is known to vary with elevation (Bowden & Buddle 2010; Cardoso et al. 2011), it is possible that factors associated with elevation, such as temperature or vegetation structure, contributed to changes in relative abundances of species or families across field sites that then translated into major differences in guild structure. For example, Abraham (1983) found a higher proportion of some families (Theridiidae and Thomisidae), but a lower proportion of others (Dictynidae, Oxyopidae, and Salticidae), relative to our study site. Patterns of guild abundance and distribution may also have been influenced by cattle during part of this study, as some spiders are known to be particularly sensitive to livestock grazing and trampling (Warui et al. 2005).

The lack of guild response may also suggest that individual species have specific ecological requirements that cannot always be captured using a guild approach. For spiders, guild membership is usually taxonomically based, since spider hunting strategies are thought to emerge at the family level (Post & Riechert 1977). However, many suggest that these generalizations are not entirely applicable to all species, or at all times, and that guild membership should reflect natural histories, rather than taxonomic relatedness (Hawkins & MacMahon 1989; Uetz et al. 1999). Although the use of guilds in this study revealed little about the relationship between spider hunting strategies and shrub architecture, the concept is still useful for examining competitive interactions and niche relations in ecological studies or when comparing communities that vary in space and time (Hatley & MacMahon 1980; Hawkins & MacMahon 1989).

Table 2.—Summary results of a similarity of percentages (SIMPER) analysis of spider species composition among shrubs of different foliage density treatments (i.e., low, natural, or high). Results indicate average relative abundance, range of contribution (%) to Bray-Curtis dissimilarities and pairwise comparisons of dissimilarities among treatments. Only species that consistently contributed ≥ 5% are shown.

Species	Low	Natural	High	% Contribution
P. clemata	25.98	25.46	18.62	12–15%
P. histrio	11.82	13.22	13.92	11–12%
E. pepinensis	5.62	8.91	13.16	7–9%
M. foxi	9.59	4.30	6.31	7–9%
O. scalaris	5.87	8.91	8.55	7–8%
E. reticulata	6.99	8.36	5.22	7–8%
D. nigra	4.36	5.63	7.01	6–7%

	Low vs. Natural	Low vs. High	Natural vs. High
Average dissimilarity (%)	65.46%	69.29%	57.48%

Table 3.—Summary results of a similarity of percentages (SIMPER) analysis of spider family composition among shrubs of different foliage density treatments (i.e., low, natural, or high). Results indicate average relative abundance, range of contribution (%) to Bray-Curtis dissimilarities and pairwise comparisons of dissimilarities among treatments. Only families that consistently contributed ≥ 5% are shown.

Family	Low	Natural	High	% Contribution
Salticidae	34.02	33.01	29.12	16–20%
Philodromidae	21.19	23.88	28.11	18%
Dictynidae	12.20	13.36	9.03	13–15%
Araneidae	10.16	5.46	6.82	12–13%
Oxyopidae	6.43	10.19	9.84	11–14%
Theridiidae	7.06	7.78	10.56	11–13%
Thomisidae	5.46	3.47	2.38	6–7%
Gnaphosidae	3.49	2.85	4.15	6%

	Low vs. Natural	Low vs. High	Natural vs. High
Average dissimilarity (%)	49.35%	50.96%	38.97%

Results from this study suggest that prey availability is also important in determining spider abundance and species riehness. Spiders may have responded to higher prey densities by either increasing prey consumption, thereby influencing rates of survival, development, and/or fecundity, or by simply migrating from areas of low prey availability to areas of high prey availability (Riechert 1974). Positive relationships could also reflect shared microhabitat preferences or physiological constraints (Riechert 1974; Bonte & Mertens 2003; Horváth et al. 2005), especially considering that prey availability was also positively associated with shrub foliage density. Furthermore, because some spiders are known to ignore prey significantly smaller or larger than they themselves are (Nentwig & Wissel 1986), and are capable of assessing nutritional quality of potential prey (Mayntz et al. 2005), it is also possible that true resource availability was never captured and the importance of prey availability was exaggerated. Since our measure of prey availability did not account for actual prey taken by spiders, future studies should incorporate observations of prey consumption to better understand prey importance for spiders.

Our results demonstrate that shrub architecture and prey availability, considered together, are better predictors of spider density and species richness than either variable considered independently. In addition, shrub architecture was a major factor governing spider diversity (H′) and community composition. However, since potential prey densities were also influenced by changes in shrub architecture, the effect of shrub arehitecture on spider communities may instead be operating indirectly via effects on prey availability, rather than directly. While not addressed here, future studies should explicitly evaluate the role of prey availability in mediating the relationship between shrub architecture and spider communities.

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Appendix 1.—List and numbers of taxa other than spiders collected from sagebrush at Hardware Ranch WMA, northern Utah, 2007–2008. Values represent pooled numbers collected from shrubs across all treatment combinations and sampling dates. An asterisk (*) indicates superfamily rank.

Order	Family	Total number collected
Acari		144
Archaeognatha	Machilidae	11
Coleoptera	Buprestidae	4
	Carabidae	26
	Cerambycidae	1
	Chrysomelidae	1649
	Coccinellidae	128
	Curculionidae	19
	Dermestidae	11
	Elateridae	1
	Histeridae	18
	Melyridae	66
	Mordellidae	5
	Searabeidae	1
	Staphylinidae	1
	Tenebrionidae	1
Collembola	Entomobryidae	5
	Sminthuridae	53
Dermaptera	Forficulidae	2
Diptera	Bombyliidae	1
	Cecidomyiidae	14
	Chironomidae	12
	Chloropidae	68
	Culicidae	2
	Phoridae	18
	Pipunculidae	3
	Sarcophagidae	1
	Sciaridae	27
	Simuliidae	10
	Tachinidae	9
	Tephritidae	35
	Ulidiidae	8
Hemiptera	Anthocoridae	4
	Cercopidae	109
	Cicadellidae	3049
	Dictyopharidae	24
	Lygaeidae	42
	Membracidae	59
	Miridae	2967
	Nabidae	253
	Ortheziidae	7
	Pentatomidae	23
	Psyllidae	47
	Reduviidae	11
	Rhopalidae	3
	Scutelleridae	5
	Tingidae	39
Hymenoptera	Braconidae	28
	Chalcidoidea *	201
	Chrysididae	2
	Cynipoidea *	18
	Halictidae	1
	Ichneumonidae	2
	Vespidae	1
Lepidoptera	Lycaenidae	7
	Noctuidae	299
	Nymphalidae	2
	Pterophoridae	1
Mantodea	Mantidae	1
Neuroptera	Chrysopidae	3
	Hemerobiidae	3
	Myrmeleontidae	1
	Raphidiidae	8
Odonata	Coenagrionidae	2
Orthoptera	Acrididae	57
	Rhaphidiphoridae	2
	Tettigoniidae	32
Psocoptera	Liposcelidae	100
	Psocidae	75
Thysanoptera		87
Total		9929

Appendix 2.—List and numbers of spider taxa collected from sagebrush at Hardware Ranch WMA, northern Utah, 2007–2008. Values represent pooled numbers of adult specimens collected from shrubs across all treatment combinations and sampling dates.

Family	Species	Total number collected
Araneidae	*Aculepeira packardi* (Thorell 1875)	1
	Hypsosinga funebris (Keyserling 1892)	1
	Metepeira foxi Gertsch & Ivie 1936	60
Dictynidae	*Dictyna idahoana* Chamberlin & Ivie 1933	6
	Emblyna piratica (Ivie 1947)	57
	Emblyna reticulata (Gertsch & Ivie 1936)	85
Gnaphosidae	*Micaria gertschi* Barrows & Ivie 1942	31
	Unidentified	1
Linyphiidae	*Erigone dentosa* O. P.-Cambridge 1894	9
Lycosidae	*Pardosa utahensis* Chamberlin 1919	7
Mimetidae	*Mimetus aktius* Chamberlin & Ivie 1935	2
Oxyopidae	*Oxyopes scalaris* Hentz 1845	133
Philodromidae	*Ebo pepinensis* Gertsch 1933	157
	Philodromus histrio (Latreille 1819)	161
	Philodromus sp.	3
	Thanatus formicinus (Clerck 1757)	27
	Tibellus oblongus (Walckenaer 1802)	12
Salticidae	*Evarcha hoyi* (Peckham & Peckham 1883)	2
	Habronattus americanus (Keyserling 1885)	42
	Pelegrina clemata (Levi & Levi 1951)	690
	Phidippus johnsonii (Peckham & Peckham 1883)	24
	Sassacus papenhoei Peckham & Peckham 1895	18
	Synageles idahoanus (Gertsch 1934)	55
Theridiidae	*Chrysso pelyx* (Levi 1957)	1
	Dipoena nigra (Emerton 1882)	81
	Theridion petraeum L. Koch 1872	22
	Theridion sp.	7
Thomisidae	*Mecaphesa lepida* (Thorell 1877)	3
	Xysticus cunctator Thorell 1877	1
	Xysticus gulosus Keyserling 1880	2
	Xysticus montanensis Keyserling 1887	43
Total		1744